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Nesting Biology and Mature Larva of the Bee *Idiomelissodes duplocincta* (Hymenoptera: Anthophoridae: Eucerini)

JEROME G. ROZEN, JR.¹

ABSTRACT

The communal nest of *Idiomelissodes duplocincta* (Cockerell) is described from Arizona. Features examined are nest architecture, cell orientation and structure, cocoon construction, fecal placement, and cleptoparasitism by *Triepeolus* (Nomadinae). Nesting behavior characteristics of *Idiomelissodes* are discussed in relation to those of other Eucerini and found to be similar. The

mature larva of *I. duplocincta*, similar to larvae of other Eucerini, is described and illustrated. Anatomical structures of the mature larvae of the Eucerini including *Idiomelissodes* are analyzed in terms of their plesiomorphic/apomorphic states, in anticipation of an investigation of the phylogenetic relationships of the taxa within the Anthophoridae based on larvae.

INTRODUCTION

Idiomelissodes is a monotypic eucerine genus from the deserts of California to New Mexico and southward into northern Mexico (Hurd, 1979). Zavortink (1975) discussed the behavior, distribution, and host plants of *Idiomelissodes duplocincta* (Cockerell), but nothing has been recorded about its nesting behavior or immature stages. The following data on its nest and mature larva are offered

in the hope that they will eventually contribute to an understanding of the phylogenetic relationships of the Eucerini (Anthophorinae) with other anthophorid tribes and subfamilies.

LaBerge (1956) proposed *Idiomelissodes* as a subgenus of *Melissodes*, and the following year (1957) accorded it generic status. Subsequently he (LaBerge, 1961) placed it as a

¹ Curator, Department of Entomology, American Museum of Natural History.



Fig. 1. Nesting site of *Idiomelissodes duplocincta* at 5 mi east Sahuarita, Pima County, AZ.

subgenus of *Svastra*. More recently Michener and McGinley (in prep.) considered it related either to *Svastra* or *Melissodes*.

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BIOLOGY

DESCRIPTION OF SITE: A single nest of *Idiomelissodes duplocincta* was discovered in the ground on August 11, 1990, at 5 mi east of Sahuarita, Pima County, AZ (fig. 1). The soil surface was horizontal, and the substrate consisted of fine moist sand with few rocks or pebbles at the cell level. Barrel cactus, *Ferocactus* sp., the principal pollen source for this species, grew within 30 m of the nest and was blooming when the nest was first found. The open nest entrance was near a small, nearly dead bush of *Larrea tridentata* but was neither hidden nor shaded by the bush. The opening, without tumulus and approximately 6 mm in diameter, descended obliquely.

Pollen-laden females were entering the nest during midmorning, and I captured four departing females with an inverted plastic drinking glass. No precise estimate can be made of the number of females occupying the nest, but the flight activity at the entrance would seem to indicate that the numbers were low, certainly in the tens rather than in the hundreds. Because captured individuals showed no wing wear (suggesting that the nesting season had just started), I was surprised to find the entrance completely covered with soil and no adult activity when I returned 15 days later, on August 26. I excavated the nest and found four flaccid post-defecating larvae encased in cocoons and another larva starting to defecate.

NEST ARCHITECTURE: Immediately below the surface, the entrance tunnel divided, both branches extending obliquely downward. Each was 6 to 6.5 mm in diameter, as were all tunnel sections discovered below them. Both ended at a depth of 5 to 8 cm, presumably because they were blocked with fill. Ex-

cavating further, I encountered a number of sections of unfilled tunnel to a depth of 30 cm and at a horizontal distance of as much as 65 cm from the nest entrance. Some sections, partly filled or completely open, could be traced for as much as 15 cm; these curved in all directions from vertical to horizontal. Tunnels divided and in some cases one branch was walled off by a partition from the other. These observations suggest that the nest, when active, was large and consisted of a maze of tunnels winding in all directions, filled in places, presumably by material excavated from new branches and cells.

All cells were vertical or nearly so, symmetrical around their long axes, arranged singly at the ends of branches that gradually curved downward to them. Cells were widely scattered throughout the nest area, there being no concentration of them in any one place. Cells ranged in depth from 24 to 36 cm ($N = 5$). Cell walls were at most slightly more consolidated than the substrate, and the walls did not seem to be plastered into a slightly larger, excavated cavity, as is the case with the Emphorini. The smooth inner surface was dark chocolate brown when first excavated, darker than the substrate, and was coated with a waterproof, transparent, shiny film that could easily be floated from a section of cell wall submerged in water. When dry, the cell's inner surface became pale like the substrate. One open cell containing partial provisions was 14.5 cm long from the entrance constriction to cell bottom. A cocoon and feces in another cell were 16.0 mm long, and the distance from the top of the feces to cell bottom in the cell containing a postdefecating *Triepeolus* larva was 14.0 mm long. Three cells measured 6.5–7.0 mm in maximum diameter, about halfway between the top and bottom of the cells. In side view, cell walls seemed slightly curved rather than straight and parallel. Cells appeared unusually elongate for their diameter, as seems to be characteristic of all eucerines.

Several vacated cells from previous generations indicated that the nest served more than one generation.

COCOONS: All cocoons consisted of an opaque upper part composed of the feces usually intermixed with silk and a lower part constructed of semitransparent silk without

feces and containing the immature *Idiomelissodes* more or less visible from the outside. They did not differ significantly on the outside from those illustrated for other eucerines (Linsley et al., 1955; Thorp and Chemsak, 1964; Rozen, 1964, 1969; Miliczky, 1985). The sides and bottom were closely pressed to the cell surface and assumed the shape of the cell. Here the cocoon fabric was sheetlike; that is, it formed an even, plasticlike surface presumably resulting from the threads or ribbons of freshly deposited silk fusing with others. There were only occasional silk threads in the fabric. The outer cocoon surface was dull tan and semitransparent, but one (or more) inner layer was clear and cellophane-like. Although it consisted of these layers that could be peeled, the cocoon material formed a single sheet with no air spaces between layers. Because cocoon walls lacked feces, the soft cocoons tended to lose their shape when extricated from the cells.

The upper surface of the cocoon lumen was a dome of silk pressed to the lower surface of the fecal mass. Its periphery was fabric similar to the cocoon wall; however, the center of the cocoon top, an area approximately 3 mm in diameter, was different; it consisted of several layers of thin silk, sheetlike in some places and threadlike in others, so that irregular fenestrations were obvious in the lowermost layer. Spaces existed between these layers so that the thickness of the center part of the cocoon top was approximately 0.25 mm. It seems likely that fenestrations appeared in the several other layers of the cocoon top and consequently allowed passage of gases between the cocoon lumen and the cell closure, through the feces.

Because fecal material incorporated some threadlike and sheetlike silk, the *Idiomelissodes* larva must defecate as it starts the cocoon, but obviously the cocoon spinning process continued after the alimentary tract had been voided, thus explaining the silk layer roofing the lumen of the cell. The pointed abdominal segment X of the mature larva presumably is an adaptation permitting the larva to extend the posterior part of the body upward and apply feces *en masse* to the top of the cell.

PARASITISM: A single curved, quiescent, postdefecating *Triepeolus* larva (species un-

known), leaning against the cell wall and resting on the tip of its abdomen, was encountered in one cell. It has applied most of its feces to the lower surface of the closure, but thin smears extended on the cell walls to the bottom. No cocoon was present, as is also characteristic of other Nomadinae. The head capsule of the first instar with features similar to other species of *Triepeolus* (Rozen, 1989b) was found fixed by chance to the head capsule of the last instar. The presence of the first instar head capsule and the general appearance of the mature larva surrounded by feces closely resembled the photographs of *Triepeolus helianthi* (Robertson) in nests of *Melessodes agilis* Cresson (Parker et al., 1981).

DESCRIPTION OF THE MATURE LARVA OF *IDIOMELISSODES DUPLOCINCTA*

Figures 2–8

The format and terminology used here follow those proposed by Rozen and Michener (1988), and the description is comparative with earlier ones of eucerine larvae presented in Rozen (1965).

DIAGNOSIS: Mature eucerine larvae including those of *Idiomelissodes duplocincta* can be distinguished readily from larvae of other anthophorid groups on the basis of any of the following three character sets. The labrum (fig. 4) is extremely broad, bears a pair of low but distinct tubercles apicolaterally, and possesses a more or less trilobed apical margin. Mandibles (figs. 6–8) are distinctive in that they are apically bifid, with acute teeth, have their dorsal adoral surface set off from the apical concavity by a ridge, and possess (at least in some species) long spicules on the dorsal surface. Abdominal segment X (fig. 2) is small, more or less triangular in lateral view, and apically pointed.

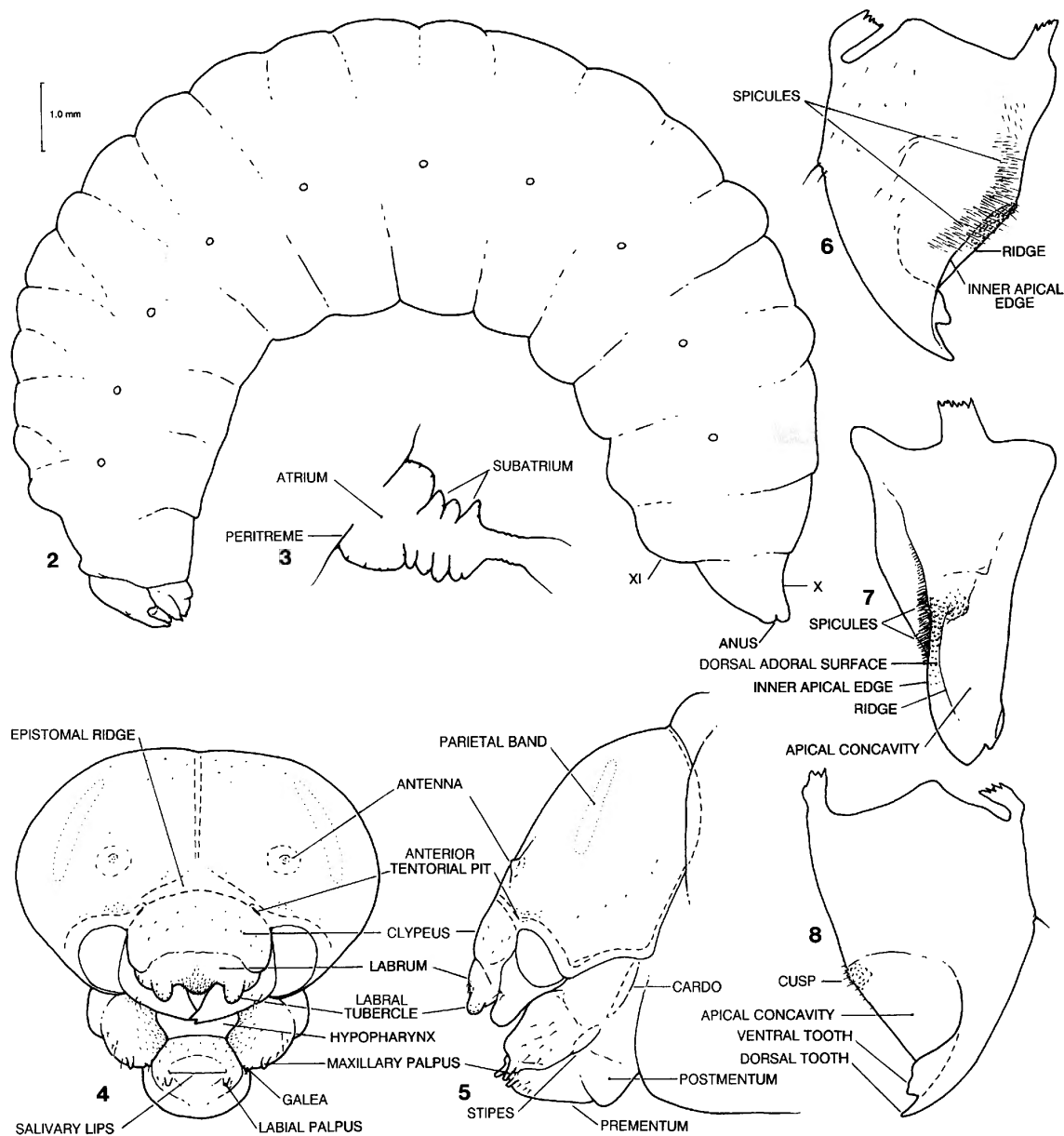
Differences among known eucerine larvae are slight. The labral tubercles of *Idiomelissodes* are more pronounced than those of other larvae available to me, but it is impossible to compare them with literature accounts of other taxa. Rozen's (1965) key to eucerine larvae known at the time of the study was based on mandibular features; future com-

parative studies will probably find mandibles a valuable source of diagnostic features.

HEAD (figs. 4, 5): Integument of head capsule with scattered sensilla that are not obviously setiform; sensilla of mouthparts mostly setiform. Integument weakly pigmented except apices of mandibles dark, palpi faintly pigmented, hypostomal ridge moderately dark.

Head size (fig. 2) small compared with rest of body; head capsule distinctly wider than maximum length from vertex to lower clypeal margin. Tentorium strongly developed, possessing dorsal arms; anterior pits moderately low on face, not immediately adjacent to mandibular precoxae; posterior tentorial pit normal in position, at junction of posterior margin of head and hypostomal ridge; posterior thickening of head capsule well developed, only slightly curving forward medially as seen in dorsal view; posterior margin of head normal in position; median longitudinal thickening of head capsule well developed, extending downward about as far as epistomal ridge; hypostomal ridge well developed, without ramus, moderately short, forming nearly 90° angle with posterior margin as seen in lateral view; pleurostomal ridge well developed; epistomal ridge well developed except fading somewhat from above medially (fig. 4); epistomal depression inconspicuous. Parietal bands faint. Antennal prominence weakly developed; antennal disk moderate in size; antennal papilla small, bearing three sensilla. Vertex evenly rounded as seen from side (fig. 5), without unusual projections or tubercles; clypeus broad as seen in frontal view (fig. 4), similar to that of other eucerines; frontoclypeal area in lateral view normal, not produced beyond labrum. Labrum in lateral view not strongly projecting beyond clypeus; labral sclerite not evident; labral tubercles (figs. 4, 5) pronounced, widely separated, downward projecting; labral apex (fig. 4) in frontal view strongly trilobed (even discounting tubercles); median lobe with fine elongate spicules; epipharynx only vaguely produced medially, with two paramedian patches of elongate, setalike spicules overlaying similar spicules on dorsal surface of closed (or partly closed) mandibles.

Mandible (figs. 6–8) large, robust; dorsal



Figs. 2–8. Mature larva of *Idiomelissodes duplocincta*. **2.** Predefecating larva, lateral view. **3.** Spiracle, side view. **4, 5.** Head, front and lateral views, respectively. **6–8.** Right mandible, dorsal, inner, and ventral views, respectively. Scale refers to figure 2.

mandibular spiculation conspicuous (fig. 6) because spicules elongate; outer surface of mandible with several conspicuous seta-bearing tubercles; mandibular apex bifid, dorsal tooth projecting farther than ventral tooth; large tooth on dorsal apical edge near cusp absent; dorsal adoral surface of man-

dible separated from apical concavity by distinct ridge that more or less parallels dorsal apical edge (fig. 7); this ridge fading apically; dorsal adoral surface (fig. 7) bearing numerous small, round denticles in vicinity of cusp; these denticles becoming less pronounced apically; apical concavity well developed,

smooth except in vicinity of cusp, without spines. Labiomaxillary region produced, as in other cocoon-spinning bees, not greatly fused. Maxillary apex (fig. 4) produced only slightly mesally, spiculate; sclerotized cardo and stipes distinct but not pigmented; articulating arm of stipital sclerite distinct; maxillary palpus elongate; galea (fig. 4) small but distinct. Labium divided into prementum and postmentum; premental sclerite unpigmented, not defined; labial palpus smaller than maxillary palpus. Salivary lips well developed, projecting, forming very wide transverse slit. Hypopharynx a more or less flat surface extending from hypopharyngeal groove to buccal cavity, not strongly projecting, nonspiculate, not bilobed.

BODY: Integument without setae, extremely finely, evenly, but sparsely spiculate; body without spines or sclerotized tubercles. Body form (fig. 2) moderately elongate, but not as much as in Emphorini; intersegmental and intrasegmental lines moderately incised; dorsolateral body tubercles absent, cephalic and caudal annulets projecting about equally as seen in lateral view; lateral tubercles vaguely developed on postdefecating larva (not depicted) but not on predefecating larva (fig. 2); ventrolateral tubercles absent; venter of abdominal segment IX not produced (but this character difficult to evaluate because small, dorsally attached segment X makes segment IX appear vaguely produced ventrally); abdominal segment X elongate, pointed apically, attached to upper part of segment IX; dorsal surface without ridge; anus small, positioned apically on pointed tip of segment. Spiracles (figs. 2, 3) moderately large, without sclerites; peritreme flat; atrium not projecting above body wall, with vague rings of widely separated, sometimes pointed denticles; primary tracheal opening with collar; subatrium short, of three to five chambers, integument of which also denticulate. Male postdefecating larva with transverse cuticular scar near middle of venter of abdominal segment IX; female postdefecating larva with paired imaginal disks visible through ventral integument of abdominal segments VII–IX; sex of predefecating larva uncertain.

MATERIAL STUDIED: 2 male, 1 female postdefecating larvae, 1 predefecating larva, 5 mi

east Sahuarita, Pima Co., AZ, August 26, 1990 (J. G. Rozen).

DISCUSSION AND CONCLUSIONS

NESTING BEHAVIOR: There is a considerable amount of nesting behavior data scattered in the literature regarding this tribe (see for example citations in Hurd, 1979). Almost all of it pertains to single species (exceptions are Claude-Joseph, 1926; Janvier, 1933, 1955) and most of it is fragmentary. Two papers that made important contributions to our understanding of the range of nesting behavior in the tribe are by Linsley et al. (1955) and Miliczky (1985). Each attempted to summarize literature accounts on nesting biology; see those papers for references. Since then other studies have appeared: *Martinapis luteicornis* (Cockerell) (Rozen and Rozen, 1986); *Thygater* sp. (Packer, 1987); *Peponapis utahensis* (Cockerell) (Rozen and Ayala, 1987); and *Xenoglossodes eriocarpi* (Cockerell) (Rozen, 1989a). The statements below refer to these species as well as those addressed by Linsley et al. and Miliczky.

Both Linsley et al. (1955) and Miliczky (1985) identified a number of points of intratribal comparison regarding nesting biology of the Eucerini. (Linsley et al. also addressed intertribal comparisons, but such matters are beyond the scope of this paper.) Although some of the points (such as provisioning and egg placement) are not applicable to the present study, others form the basis for the following comments regarding *Idiomelissodes* in relation to known Eucerini:

1. Females of most Eucerini nest singly. However, in addition to communal nests in *Idiomelissodes*, such nests have been reported for two species of *Svastra* (Rozen, 1964, 1983) and one of *Melissodes* (Hurd and Linsley, 1959).

2. Nest architecture among eucerines is quite diversified, from nests with single cells to those (probably including *Idiomelissodes* although only 5 cells were unearthed) containing a number of communally nesting females with numerous cells. Cell depths also vary considerably from species to species. A nest of *Thygater analis* (Lepeletier) (Rozen, 1974) suggests that sequence of cell and bur-

row construction may be complicated and worth studying.

3. From literature accounts, Miliczky concluded that there are two methods of cell construction in the Eucerini: *either* the female excavates a large cavity and builds a wall into the space *or* the female constructs a cavity the size and shape of the cell and impregnates the wall with a hardening substance. Cells of *Idiomelissodes* appear to conform to the latter situation. However, method of cell construction in the Eucerini has not been based on observations of digging females or examination of cells in various stages of completion, but only on what is inferred from observations of completed cells in widely different substrates, some of which are more revealing than others. It is unlikely that two such seemingly dichotomous methods of cell construction exist in closely related taxa. Further study may reveal that these two apparent methods actually represent extreme examples of a single method of cell excavation.

4. Cells of *Idiomelissodes*, like those of most (but not all) other eucerines, are arranged singly (not in linear series and not grouped into clusters).

5. Cells of *Idiomelissodes*, like those of other eucerines, are vertical or nearly so. The only known exception is *Xenoglossodes eriocarpi* in which some cells appeared to be tilted about 45° from vertical.

6. Cells of all eucerines including *Idiomelissodes* are elongate relative to their maximum diameters. As Miliczky pointed out, cells of some species are described as being nearly parallel whereas cells of others appeared to have the greatest diameter below the middle. Such differences are apparently real, but, because of the difficulty in observing cell shapes, more exact quantification is necessary. Whereas cells of *Idiomelissodes* seem widest at the middle, the walls are not straight and parallel but slightly curved.

7. Cell closures of *Idiomelissodes* and other eucerines are made of soil formed into a concave spiral, as viewed from inside the cell. A remarkable exception reported by Mohamed (1974b) is that the closure of *Tetralonia lanuginosa* consists of a compact spiral of camphor-tree leaf particles and saliva.

8. In the literature, eucerine cell linings

(like the linings of many other kinds of bees) have been informally described as: waxlike, silklike, non-waxlike, varnished, and lacquered. Such terms are of little use because it is difficult to interpret what authors had in mind. Descriptions of the physical properties of linings are more helpful, but chemical composition and origin of the lining substance are most meaningful (though difficult to obtain).

9. Placement of the *Idiomelissodes* feces at the top of the cell, just below the closure, mostly before cocoon construction, is characteristic of all eucerines. Eucerine cocoons are immediately recognizable because of this feature.

10. The cocoons of *Idiomelissodes* externally are typical of those described for other species. Comparing *Idiomelissodes* cocoons with those of other species stored in the collections of the American Museum of Natural History does reveal some differences in structure, fabric texture, and shape of the multi-layered, nipplelike upper part. Such differences as well as certain similarities of eucerine cocoons compared to those of *Centris* (Rozen and Buchmann, 1990) are worthy of investigation.

11. The association of a species of *Triepeolus* with *Idiomelissodes*, reported here for the first time, comes as no great surprise considering both the large *Triepeolus* fauna (probably mostly unnamed) in the Southwest and the *Triepeolus* associations with other eucerine genera. In addition to Epeolini, parasitic bees attacking nests of eucerines belong to the Melectini (Wafa and Mohamed, 1970), Ammobatini (Bischoff, 1927; Iuga, 1950; Rozen, 1969; Rozen and McGinley, 1974), Nomadini (Bischoff, 1927; Masuda, 1940; Iuga, 1950), and apparently even *Coelioxys* (Megachilidae) (Bischoff, 1927).

MATURE LARVA: Rozen (1965) presented an account of the mature larvae of the Eucerini incorporating previous descriptions as well as firsthand treatment of representatives of four genera (*Xenoglossa*, *Svastra*, *Melissodes*, and *Peponapis*). Subsequently, LaBerge and Ribble (1966) described the mature larvae of *Florilegus condignus* (Cresson); Clement (1973), *Melissodes rustica* (Say); Miliczky (1985), *Tetralonia hamata* Bradley;

and Packer (1987), *Thygater* sp. All authors commented on the uniformity of the anatomy of mature larvae within the tribe. *Idiomelissodes duplocincta* also does not differ substantially from other tribal members.

It is impossible to interpret the phylogenetic relationships of the eucerines to other anthophorid tribes on the basis of mature larvae because immatures of many of the other tribes (especially the Exomalopsini and its presumed relatives) are unknown or are too poorly known. Nonetheless, estimates can be made in some cases as to which character states of mature eucerine larvae are apomorphic and plesiomorphic. Certain other features can be identified as being of uncertain polarity but of potential interest once their polarity has been determined. Such evaluations are possible because of treatments of other groups of anthophorids by Michener (1953), Rozen (1966, 1969), Rozen et al. (1978), McGinley (1987), and Rozen and Michener (1988) and because of a better understanding of bee larvae in general.

These evaluations, identified by the character states found in *Idiomelissodes*, are presented below. They are offered so that validity of the judgments regarding polarity can be tested and characters of undetermined polarity can be given further study, all in preparation for an investigation of the phylogenetic relationships within the Anthophoridae based on mature larvae.

1. Strongly developed tentorium and internal ridges of the head capsule. These are plesiomorphic in the Anthophoridae and probably in the Apoidea. They appear to be characteristic of most bee larvae that spin cocoons and have robust mandibles. The apomorphic condition in the family (weakly developed tentorium and internal head ridges) is characteristic only of the Nomadinae (exclusive of *Isepeolus* and *Protepeolus*).

2. Clypeus and labrum unusually broad. This feature is believed to be apomorphic. A parallel condition exists in the Anthophorini, but whether due to convergence or relationship is uncertain. The narrower clypeus and labrum in the other anthophorids is presumably plesiomorphic.

3. Labral tubercles. These are judged apomorphic in the Eucerini and seem to be homologous to those found in the Antho-

phorini and some Melectini and Ericrocini because of similar sizes and shapes and identical positions on the apicolateral angles of the labrum. Paired labral tubercles are unknown elsewhere in the family except in the Nomadinae where they are greatly elongate in first instars and apparently function in host detection (Rozen, 1989b). In last instars their position is more on the labral disc rather than on the apicolateral angles of the labrum. Labral tubercles are scarcely produced in early instars² of eucerines (Rozen, 1964, 1965). Because of these ontogenetic differences and apparent differences in position, labral tubercles of the two tribes may not be homologous.

4. Labral apex trilobed in frontal view. Because this feature appears to be unique to the Eucerini, it is thought to be apomorphic. In other anthophorid groups, the labral apex is either slightly bilobed or produced as a single broad lobe in frontal view.

5. Mandible large, robust. Mandibles of eucerines appear to be larger than those of many other bee larvae, but rather large mandibles are also found in emphorines and exomalopsines, centridines, and some xylocopines. Hence the condition in the Eucerini is plesiomorphic in the Anthophoridae at least in contrast to the extremely short mandibles of the Nomadinae.

6. Mandibular apex bifid. Most anthophorid groups as well as megachilids have bifid mandibles, an indication that this condition is plesiomorphic. Simple mandibles of

² In recent studies I have concluded that in many, if not all, nonparasitic anthophorids, the first instar is mostly encased in the egg chorion and the second instar is the stage that crawls away from the chorion (and first instar cast skin). Therefore, the young larvae of *Svastra obliqua* (Say) (Rozen, 1964) and *Xenoglossa angustior* Cockerell (Rozen, 1965) that I described were second, not first, instars. The true first instar of *Svastra o. obliqua*, covered by chorion, was depicted as an "egg at time of eclosion" in Rozen (1964: fig. 5). Wafa and Mohamed (1970), in their excellent detailed study of the life cycle of *Tetralonia lanuginosa* Klug, described the behavior and feeding activities of the "embryo." Their observations are consistent with mine regarding first instars of anthophorids, and I interpret their "embryo" to be the true first instar, which means that *T. lanuginosa* has five larval instars. The first instar of the same species described by Mohamed (1974a) presumably is actually the second.

mature larvae of parasitic long-tongued bees are probably ontogenetic holdovers from earlier instars and are derived.

7. Dorsal adoral surface of mandible separated from apical concavity by distinct ridge. This feature appears to be unique for the Eucerini and is an immediate diagnostic feature. Hence it appears to be apomorphic, but the shape of the adoral apical surfaces of anthophorid mandibles varies greatly even among pollen-collecting taxa. In some (Centridini, Anthophorini), it is a large, apically rounded scoop often with a small subapical tooth; in others (Exomalopsini, some Emphorini), it is narrow with two acute apical teeth with a ventral concavity and produced, dorsal adoral ridge above. The polarity of these and other variations is not understood at present, although the bifid apex is also shared by the megachilids and may therefore be a primitive component.

8. Labiomaxillary region produced, not greatly fused, with distinct prementum and postmentum, and well-developed salivary lips and palpi. Throughout the Apoidea, these attributes are indicative of a larva able to spin a cocoon and are regarded as plesiomorphic because of the unlikelihood of this combination repeatedly arising *de novo*. A recessed and fused labiomaxillary region and reduced or absent salivary lips and palpi, characteristic of noncocoon-spinning, are derived. The derived condition has evolved many times and is found in most families of bees.

9. Maxillary apex produced slightly mesally. Polarity of this character is uncertain. Strongly bent and produced maxillary apex, found in the Emphorini and Anthophorini and also in some members of other families of bees (e.g., *Ctenoplectra*, *Trachusa*, *Dioxys*, *Fideliinae*), may be plesiomorphic (as assumed by Rozen, 1969). However, if primitive, why is it never associated with another primitive feature of the maxillary apex of some bees, i.e., presence of a galea, found, for example, in *Centris*, Eucerini, *Meganomia*, Melittinae? A comprehensive study is required of the following features: the bending and production of the maxillary apex, the production (or lack thereof) of the hypopharynx, presence or absence of a galea, the production (or lack thereof) of the epipharynx, and the adoral mandibular attributes.

The structures that surround the larval mouth obviously function together and therefore their form and structure must be interrelated. Understanding their functioning and anatomical interrelatedness may give insight into the polarities of the character states of each of the structures.

10. Articulating arm of stipital sclerite distinct. Discussed in Rozen and Michener (1988), this is an obviously primitive feature, and its absence is therefore apomorphic.

11. Galea distinct. This is a plesiomorphy as discussed under 9, above.

12. Salivary lips very wide. The unusually wide salivary lips of eucerines, probably linked with the broad labrum and clypeus, are judged apomorphic, as their width is not equaled by cocoon-spinning larvae of other families or of other anthophorids except perhaps for some *Centris*.

13. Hypopharynx a flat surface. The hypopharynx of many other anthophorid groups is bilobed and strongly bulging. The polarities of these states are uncertain, but may be revealed through an investigation described under 9, above.

14. Body form moderately elongate. This feature is plesiomorphic in relation to the extremely elongate bodies of larval Emphorini.

15. Venter of abdominal segment IX not produced. Both produced (e.g., Exomalopsini and Emphorini) and nonproduced (e.g., Eucerini, Anthophorini, and Xylocopinae) conditions are found in the Anthophoridae. The polarity of the character is indeterminate at this time. A produced venter of abdominal segment IX may be functionally associated with larvae crawling around semisolid food masses in the two tribes listed above.

16. Abdominal segment X elongate, pointed apically, attached to upper part of segment IX. The elongate, pointed condition of abdominal segment X in the Eucerini is an autapomorphy, presumably correlated with placing feces at the top of vertical cells.

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